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ON THE FORMATION OF PHYSIOLOGIC RACES IN PLANT PARASITES

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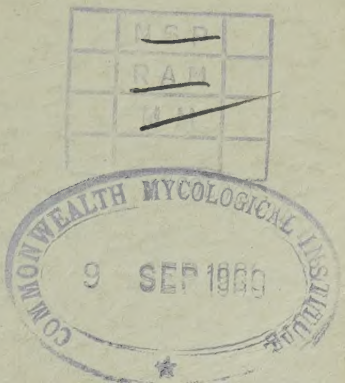

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ON THE FORMATION OF PHYSIOLOGIC RACES IN PLANT PARASITES

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ABSTRACT

New physiologic races can be produced by mutation, hybridization or heterokaryosis. The genetics of the host parasite relationship can be explained on the basis of the gene-for-gene hypothesis of FLOR.

Resistance breeding is an important agent in the appearance of a new race and in the evolution of pathogenicity.

In America the resistance breeding in wheat is conducted along the following lines:

1. Searching for sources of resistance by testing collections of varieties and hybrids.
2. Crossing good agricultural varieties (recurrent parents) with resistant parents and making subsequent backcrosses of the hybrids with the recurrent parents. In this way lines are developed which are similar in many characters but different in their genetic constitution as concerns the resistant genes.
3. This program executed several procedures can be applied:
   a. Production of resistant substitution lines which can replace varieties having lost their resistance.
   b. Production of multiline varieties composed of lines differing in their genes for resistance.
   c. Distribution of resistance genes over the agricultural regions so that every district has its own type of resistance.

The author considers it desirable to adapt these procedures to European situations. For Europe the most suitable application of the new aspects seems to be the multiline variety.

1. INTRODUCTION

Some 50 years ago the Dutch scientist HUGO DE VRIES said: "The origin of species is an object of experimental investigation" (28). This maxim paved the way for many new lines of research.

As a variant of DE VRIES' statement we would use the same motto for this article: "The origin of physiologic races of fungi is an object of experimental investigation".

Some results and implications of experimental research in this field (which is mainly conducted in America) will be given in this article.

* Lecture held at the 2nd EUCARPIA Congres, section Cereals, July 1959 at Cologne.

2. Physiologic specialization

When inoculating a set of host plants H_1, H_2, etc. with different isolates of a parasite P_1, P_2, etc. we may expect various reactions. In routine work these reactions have been standardized to reaction types, indicated by symbols (table 1). A differential set of host plants inoculated with one given isolate of a parasite presents a set of reaction types or a *reaction spectrum*. When isolates differ in reaction spectrum we speak of physiologic specialization of the parasite. Isolates with similar reaction spectra are classified into taxonomic units, one of them being the physiologic race, or briefly, race.

Table 1. Diagram illustrating the principle of reaction spectra

		Host differentials				
		H_1	H_2	H_3	H_4	H
Parasite isolates	P_1	+	—			
	P_2	—	+			
	P_3					
	P					

Reaction types
+ = susceptible
— = resistant

Rows reaction spectrum of host plants characterises isolate or race of the parasite

Columns reaction spectrum of races may characterise genetical composition of the resistance of the host plant

A differential set of varieties can be composed for special purposes or local conditions. Several differential sets have been accepted internationally e.g. those of the cereal rusts. A physiologic race is called virulent when it causes severe symptoms on a differential variety. The opposite is an avirulent race. An aggressive race attacks many varieties of a differential set (table 2).

Table 2. Diagram illustrating the terms virulent and aggressive

	H_1	H_2	H_3	H_4	
P_1	3	3	1	2	not virulent, aggressive
P_2	4	4	4	4	virulent, aggressive
P_3	0	0	0	4	virulent, not aggressive
	reaction types				

Reaction types from 0 = resistant reaction
to 4 = highly susceptible reaction

It should be clearly understood that a physiologic race is an artificial unit based on a small number of differential varieties.

In most cases the infection spectrum of a differential set does not give us any information on the genetical background of a race. A large number of genetically different biotypes may occur in one race.

3. The genetic background of physiologic specialization

The symptoms of a host plant caused by a parasite are controlled by the genetic constitution of both host plant and parasite and also by environmental conditions. Flor (8, 10) proposed a system in which the host-parasite reaction is not determined by complete genomes but by one gene pair of the host and one gene pair of the parasite (table 3). This system will be indicated here as the gene-for-gene hypothesis of Flor. Flor has argued his gene-for-gene hypothesis in a most skilfull way. He worked with flax rust and this enabled him to perform the genetical analysis of both flax and the rust parasite. In flax resistance is dominant, and in flax rust virulence as a rule is recessive. Flor identified 25 genes for resistance, occurring in 5 loci, two of which are coupled. In one locus up to 10 alleles for resistance may be localized. The rust has 25 genes for virulence, one virulence gene for every resistance gene in the host. Coupling has been observed.

Table 3. Diagram illustrating gene-for-gene interaction in locus 1

	A_1A_1	A_1a_1	a_1a_1	Rust
R_1R_1	—	—	+	
R_1r_1	—	—	+	
r_1r_1	+	+	+	
Flax				

Flax R = gene conditioning resistance, dominant
r = gene conditioning susceptibility, recessive
Rust A = gene conditioning avirulence, dominant
a = gene conditioning virulence, recessive
Reaction types + = susceptible reaction
— = resistant reaction

Many observations support a more general validity of the gene-for-gene relationship. Hybridization experiments in *Venturia inaequalis*, the apple scab organism, seem to conform the gene-for-gene hypothesis (16); however, hybridization experiments with the host plant have not yet been made. The Black-Mastenbroek-Mills model for the genetics of *Phytophthora*-resistance (2) and a similar model for *Cladosporium fulvum*-resistance in tomatoes (6) do not contradict the gene-for-gene hypothesis, although in the last case no hybridization experiments have been performed with the parasite. The first results in hybridization experiments with *Phytophthora infestans* (23) might be explained with the gene-for-gene hypothesis.

Assuming the gene-for-gene hypothesis to be correct it should be pointed out that in this context resistance is meant to be a race-specific-resistance. Race-specific-resistance should be distinguished from the more general forms of resistance, for example the incubation resistance ("Inkubationsresistenz") to *Phytophthora* of some potato varieties, as described by Rudorf (22). The race-specific-resistance of the host is always complemented by the variety-specific-virulence of the parasite.

4. The variability of physiologic races

Mutation

Mutation is generally accepted to be the main cause of hereditary variation. For the present purpose we are interested only in mutations of pathogenicity and particularly in those increasing pathogenicity, or, more precisely, aggressiveness.

We can distinguish two groups of fungi, according as they are haploid or diploid in the pathogenic stage. *Venturia inaequalis*, the apple scab fungus, is an example of a haploid pathogen. In this fungus mutations are frequent, most of them being deficiency-mutations. Often the pathogenicity is lost. However, sometimes this loss is a result of epistasis of a deficiency gene affected by mutation over the virulence gene that is not affected by mutation. Hybridization experiments proved the pathogenic factor to be intact (3, 16, 17). Mutations of this type, producing loss of pathogenicity, are of common occurrence in fungus cultures. Increase of aggressiveness, presumably by mutation, has been observed in tomato leaf mould, *Cladosporium fulvum* (1).

In diploid or dikaryotic fungi we must take account of heterozygosity. The avirulent heterozygote *Aa* can mutate into the virulent homozygote *aa*. The problem is to prove the increase in aggressiveness. This has been realized by Flor (9, 12), who worked with clones of flax rust which were heterozygous in many loci. He found mutants with increased aggressiveness after artificial and after natural mutation. The number of mutants was small, but several occurred more than once. From Flor's data we may derive a natural mutation frequency of approximately 1:100,000. The natural mutations could be reproduced by induced mutation. The results of Flor are significant. They show that mutants occur with high frequency and also indicate that some genes are more susceptible to mutation than others.

Mutability of genes for virulence is not a constant factor. This conclusion has been corroborated by other observations. For instance race B_6 of barley mildew has been first described in Germany in 1937. It originated probably as a mutant in a glasshouse. In 1953 and in 1955 it appeared spontaneously in a glasshouse at Halle in B-group material. B_6 is more aggressive than other races of the B-group and it is characteristic for its virulence on *Hordeum spontaneum nigrum*, a parent used in breeding programmes for resistance to mildew (21).

Recently it has been found that in *Phytophthora* races avirulent to the resistance gene R_4 of *Solanum demissum* mutations showing virulence to gene R_4 occur spontaneously with a high frequency (13).

These examples show the importance of the mutability of genes for virulence. The conclusion is that there is no sense in using some race-specific resistant parent when it is expected that soon a virulent gene may appear in a mutable locus.

Mutation may give rise to a recessive gene for virulence which cannot show up in diploid or dikaryotic pathogens, as it is accompanied by a dominant gene for avirulence. The pathogen may become homozygous for the virulent gene by hybridization or by heterokaryosis. Consequently we should investigate the possibilities of hybridization and heterokaryosis.

Hybridization

Hybridization is an important source of genetical variation. The principle of race formation by means of hybridization can be explained with the aid of the gene-for-gene relationship. In haploid organisms the simplest way of race formation by hybridization is as follows:

Race:	1		2				
Genes:	a_1	A_2	× A_1	a_2			
			↓				
Genes:	a_1	A_2	+ A_1	a_2	+ A_1	A_2	+ a_1 a_2
Race:	1		2		0		1,2

In this and in the following example the loci have been numbered. The races are characterised by the numbers of the susceptible loci, as is usual in *Phytophthora* work. In both the examples avirulence (A) is dominant, virulence (a) being recessive.

In diploid and dikaryotic organisms the simplest way of race formation is that of the "self-fertilization" of a heterozygote:

Race:	1			1			
Genes:	a_1a_1	A_2a_2	×	a_1a_1	A_2a_2		
			↓				
Genes:	a_1a_1	A_2a_2	+	a_1a_1	A_2A_2	+	$a_1a_1a_2a_2$
Race:	1			1			1,2

The diagrams are valid only when the gene-for-gene hypothesis is correct and on condition that the genes are independent. In general the situation is more complicated especially through coupling. For instance coupling of non-pathogenic genes has been shown in the apple scab fungus (16) while coupling of genes for virulence in flax rust is suggested by hybridization and mutation experiments (9, 10).

Interaction of genes may complicate the picture. In the haploid apple scab fungus one gene for virulence can be epistatic over the other one (16). Epistasis has also been found in flax rust. In stem rust of oats JOHNSON found a case in which virulence was determined by two complementary genes, both of which should be present in a homozygous recessive state (14). The gene-for-gene relation becomes less clear as gene interaction complicates the picture. It can be assumed that the genetics of pathogenicity cover a wide range of possibilities from gene-specific virulence to polygenic pathogenicity.

Another complication is the occurrence of polyploidy in the parasite: the haploid number of chromosomes in oat crown rust is 3, in stem rust it is 6 (18). As a last complication we may mention cases of matrocliny among others found in oat stem rust (14).

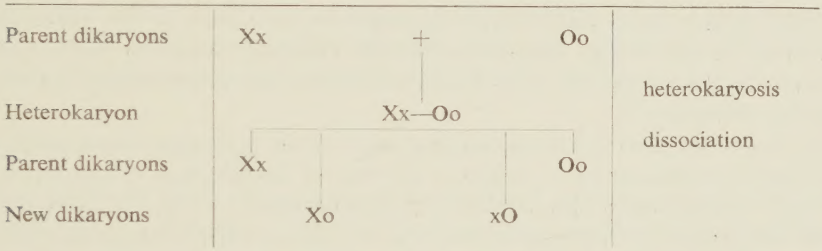
To evaluate the significance of hybridization for the origin of races we should know the importance of the sexual stage in the life cycle of the fungus. One extreme is the variable yellow rust of wheat of which no sexual stage is known. The other extreme is found in smut, both loose smut (*Ustilago tritici*) and covered smut (*Tilletia caries*) of wheat, in which no asexual propagation occurs. Flax rust takes an intermediate position: a series of asexual propagation cycles alternates every year with a sexual

cycle. It is evident that in the case of smut we cannot expect stable races since the causal organism is a cross-fertilizer. The races should be regarded as populations. Likewise flax rust has no stable races (except in glasshouses) but consists of phenotypically homogeneous populations with a wide genetic plasticity. In stem rust of wheat where the sexual phase takes place on the alternate host, the barberry, the situation is different. Race formation occurs mainly by hybridization on the alternate host. Once a new race is formed, however, it is able to live for years without passing through another sexual phase.

Heterokaryosis

Whereas hybridization implies a sexual process, comparable results can be obtained by means of heterokaryosis, a process whereby two hyphae anastomose and exchange nuclei, or parts of nuclei (parasexual recombination).

TABLE 4. DIAGRAM ILLUSTRATING HETEROKARYOSIS (EXPLANATION IN TEXT)



Formation of a new race by exchange of nuclei between two dikaryotic mycelia.

The diagram (table 4) represents heterokaryosis of two dikaryons. The letters X, x, O and o each represent one nucleus, capital letters denoting the +, the small types the −nucleus. In this diagram heterokaryosis gives rise to one new race. More complicated diagrams are possible since some genes for virulence can be associated with the + as well as with the − nucleus. So far we have assumed exchange of nuclei, but it is well-known that two seemingly independent nuclei may interchange genetic material. Somatic recombination without a sexual process (parasexual recombination) is realized in fungi and presents the same range of possibilities as the better known sexual recombination. Exchange of pathogenicity genes between nuclei has been indicated by the work of BUXTON on *Fusarium oxysporum* (5a).

The formation of new races by means of heterokaryosis has been shown in stem rust of wheat (19). A heterokaryon with three or four nuclei has been isolated. This heterokaryon behaved as a new race which was demonstrated by its virulence towards the normally resistant differential variety Khapli. This polykaryotic race was not stable: it dissociated, that is, it lost some of its superfluous nuclei. This loss of nuclei resulted in a loss of virulence to Khapli.

After 25 generations all polykaryons had disappeared. In the remaining dikaryons the two parent races were present and also two new races with intermediate characters. FLOR showed asexual formation of a new race, presumably by heterokaryosis, in flax rust (11). The frequency of heterokaryosis in nature is not well known, but the formation of new races by heterokaryosis seems to be reproducible.

From the foregoing statements it is clear that we should expect a tremendous number of races to be produced in some pathogens. However, the actual number of races is rather restricted: apparently 99 % have too small a chance to survive and settle down. Resistance breeding is the main factor governing survival and settling of new races. A variety resistant to the races present is healthy and therefore it is an ideal medium able to select the only virulent spore from a huge mass of mutated fungus spores. The resistant variety offers the mutated pathogen an excellent opportunity for multiplication without any competition.

5. The "time-race" between host and race

The epidemic of stem rust in wheat in Northern America in 1950 has been attributed to a new race of the stem rust, race 15B. Actually this race was already known for ten years but it seemed to be present in so small a quantity that nobody paid any attention to it (24, 25).

The flax variety Bison was severely damaged in the U.S.A. a few years after its introduction. It was shown afterwards that the rust race attacking Bison had been present during the test period of the variety. However, the observations had not been interpreted correctly (7).

In the two cases cited it was shown that races of the pathogen responsible for the break-down of resistance were present at the time of introduction of the new variety. The variety selected and multiplied the race. In other cases new races appeared shortly after the introduction of a new host variety as was shown with *Cladosporium fulvum* in tomatoes (1). After the introduction of a new tomato variety with a new gene for leaf-mould resistance, a new race of the fungus emerged. The time lapse between introduction of new varieties and the incidence of new races sometimes was not longer than three tomato generations. That this time lapse may be longer is shown by the history of the wheat variety Alba. This variety was introduced in Belgium in 1937. At that time Alba was resistant to yellow rust, *Puccinia glumarum*, but a severe epidemic of yellow rust in Alba occurred in 1957. The race responsible for this epidemic was not yet present in 1955; the resistance of Alba therefore lasted 19 years.

6. Origin and disappearance of races

It is interesting to know whether a race originates only once at one place (monotopic origin) or many times at several places (polytopic origin). The Alba race of yellow rust probably had a monotopic origin. The stem rust epidemic of race 15B in Northern America started from one centre. However, in the preceding years the race had been found at different places and different times; so a polytopic origin is indicated.

The disappearance of races is not difficult to explain. In general races are so specialized on their host variety that the race disappears with the disappearance of the host variety. Of course it is not possible to prove the complete disappearance of a race; however, we may find an example in the case of race 7 of yellow rust. Before World War II it was present on the wheat variety Carsten V. Though the cultivation of Carsten V has been continued for several years after the war race 7 has never since been identified from field samples. Even when a race disappears, the genes for virulence characteristic for the race may survive in a heterozygous condition in daughter races.

7. Resistance genes

The question arises how many factors for resistance can be accumulated in a host variety and how many factors for virulence can be accumulated in one physiologic race. The Black-Mastenbroek-Mills model for the resistance of *Solanum demissum* to *Phytophthora infestans* requires four factors for resistance. These factors can be present in various combinations. The four factors for virulence in *Phytophthora* can also be present in various combinations. In Mexico all these combinations have been found, even the most aggressive one, viz. race 1,2,3,4 (20). The conclusion is that Mexico not only is the gene centre of the potato species *Solanum demissum*, but also the gene centre of potato blight.

In flax Flor found 25 genes for resistance to rust. Only 5 loci are available. As flax rust has 25 genes for virulence a flax variety seldom or never is resistant to all the rust races. Now Flor found rust races with nearly all the genes for virulence in a homozygous recessive condition. So highly aggressive races are possible. However, when he studied fresh field isolates the number of virulence genes present in homozygous recessive condition appeared to be generally only one, seldom two. The dominant genes for avirulence may have some survival value (7).

8. Evolution of races

The evolution of races shows curious examples of convergence and divergence. Israel is situated in or near the gene centre of oats. It is not surprising therefore that the most aggressive and virulent races of crown rust are found in Israel.

An interesting case of convergent evolution has been recorded by Wahl (29). Race 276 of crown rust was found for the first time in Argentina. In 1953, a few years later, it was one of the most predominant races in Israel. Race 277 also was found for the first time in Argentina. In 1956 it was also found in Israel. We may assume that new races in Israel and Argentina originate independently. However, we cannot believe that this convergence is due to chance. May be the international exchange of resistant parents steers the evolution of pathogenicity in one definite direction.

Divergence exists by the side of convergence. This is evident from the numerous publications on stem rust of wheat. Sub-races can be identified when a new race has covered an area. The importance of the sub-races increases from year to year and within a short time they differentiate in their turn into sub-sub-races. This phenomenon has led to the opinion that the evolution of pathogenicity develops stepwise and at the same pace as the evolution of resistance, steered by mankind.

9. Consequences for the wheat breeder

It has been pointed out already that breeding for resistance is the result as well as the cause of catastrophic epidemics. Therefore new ways of control had to be found. The following discussion is based on stem rust work.

A search for sources of resistance is the basis of any breeding programme for disease resistance. For this purpose the United States Department of Agriculture has laid out "International Rust Nurseries", collections of several hundreds of wheat

varieties and lines. They are sown in many places in Northern and Southern America and in some places in Africa and Europe. From these collections breeders can choose the lines that are resistant in their areas and use them as parents for resistance breeding, e.g. some 50 lines. At the same time they start with a small number of varieties with a good agricultural value but susceptible to stem rust. These varieties serve as recurrent parents in a back crossing programme. The recurrent parents are crossed with the resistant parent, the resulting resistant hybrids are repeatedly backcrossed with the recurrent parent. In this way a breeder obtains for every recurrent parent a collection of some 50 resistant lines. These lines are more or less identical in morphological, physiological and agricultural characteristics but they are different in their genetic constitution as concerns the resistance to stem rust.

When this backcrossing programme has been completed two procedures are open to the breeder. The simplest procedure is to keep in store a number of so-called substitution lines of some of the most important varieties. This method has been propagated by VALLEGA in Argentina (26, 27). When a wheat variety is severely damaged by a new rust race it can be replaced immediately by a resistant line. The system of replacing lines has advantages as well as disadvantages. The new race has the opportunity of causing severe damage during one or a few years and the building up of a large inoculum may present a danger for the wheat crops of neighbouring countries. On the other hand only a few resistant lines are grown in one period and this restricts the chance of selecting new rust races.

Another procedure is applied in Mexico, Columbia and Kenya, on the initiative of BORLAUG in Mexico (4, 5). A number of backcross lines of one recurrent parent differing in the genetic constitution of their resistance but identical in all other characteristics are mixed together to form a composite variety.

In the American literature these backcross lines are called isomorphic lines; they are mixed to a multiline (multilineal or composite) variety. On the basis of the gene-for-gene relation we may assume that as a rule a new race attacks only one line. In that case the maximal yield reduction does not exceed the yield of that one line. However, the damage will be seldom very severe since the resistant lines in the mixture slow down the dispersion of the new race (see also under 10).

The building up of a large inoculum endangering the crops of neighbouring countries is minimal: When one of the lines of the multiline variety is attacked by stem rust it can easily be replaced by an isomorphic substitution line with other genes for stem rust resistance.

The two procedures, substitution of single lines and the production of multiline varieties, have been described in the literature and are now being carried out. Results have not yet been published.

A third procedure has been suggested by JOHNSON (15). He proposes to distribute the genes for resistance over the various agricultural areas in such a way that each agricultural area receives one gene for resistance, while this gene shall not be used in other agricultural areas. When such a programme has been realized, a new race will remain confined to one agricultural area only.

10. Conditions in Europe versus America

The possibilities discussed above cannot be adapted immediately to the situation in Europe. In America wheat breeding problems are focussed on breeding for stem rust resistance. In Europe, however, the main breeding objective is yield; breeding for rust resistance ranks second. An obstacle is the lack of a general organization directing the breeding on the European continent. Whereas in America breeding programmes of most states are centralized in national institutes, in Europe they are conducted by a large number of private breeders. In America the search for resistant parents is well organized while there is also a free exchange; however, in Europe most breeders search for resistant parents in their own way and they are tempted to keep them for themselves only.

It is encouraging that international co-operation also in this field is in progress. In this connection I may mention the "International European Rust Nurseries" organized by Santiago in Portugal, and the "International Yellow Rust Trials" organized by the "Netherlands Grain-Centre".

When the resistant parents have been found the three procedures described above should again be considered.

The first procedure, breeding of substitution lines, has no practical significance for Europe. European breeders try to replace a variety for another one with better resistance to diseases, better agricultural features and higher yield.

The third method, one resistance gene for every agricultural area has been realized to some extent. This could be easily demonstrated with the aid of a map of Europe indicating the areas of the most popular wheat varieties. In view of the European situation characterized by a large number of varieties and a free choice of variety by the farmer we can in fact hardly improve this local distribution of resistance genes. There remains only the second way: the production of multiline varieties.

No practical experience with multiline varieties has come to the author's knowledge. For the present we should be satisfied with experience about a mixture of varieties. In the literature it is stated here and there that a mixture of varieties in one year seldom produces more than the best of its composing varieties. However, over a number of years the average yield of the mixture generally surpasses the average yield of the composing varieties.

In order to study the phytopathological effect of a mixed culture of resistant and susceptible varieties we sowed in 1958 one ha of the wheat variety Heine VII which is very susceptible to yellow rust, one ha of Panter which is resistant to yellow rust, and one ha of a mixture comprising 50 % Heine VII and 50 % Panter. In July we established a favourable result of the mixed culture, which could be attributed to the slowing down of spore dispersal by the resistant plants of the mixture (table 5).

In Europe legal difficulties stand in the way of multiline varieties. For instance, regulations in France are very stringent: no multiline varieties are admitted. In Germany and the Netherlands multiline varieties are, with some restrictions, permitted to be entered into the official lists of varieties. However, in these countries there are no definite rules regulating admission, suppression or substitution of lines.

TABLE 5. YELLOW RUST (PUCCINIA GLUMARUM) IN A VARIETY MIXTURE

Variety	Average percentage of leaf surface attacked
Heine VII	10.5
Mixture . . . . . 50% Heine VII 50% Panter	1.3
Panter	0.0

$P < 0.01$

For practical breeding purposes the multiline variety presents technical advantages. A backcrossing programme comprising many lines with each only one gene for resistance is easier to realize then a programme involving only one line with many genes for resistance. A disadvantage of a multiline variety is the presence of many genes for resistance in one small area, which might lead to accumulated selection of new races. However, we hope that multiline varieties will slow down the speed of evolution of new physiologic races so that our crops will remain healthy.

SAMENVATTING

Fysiovorming bij parasieten van planten

Nieuwe fysiologische rassen kunnen ontstaan door mutatie, kruising of heterokaryose. Met behulp van de gen-om-gen hypothese van FLOR kan de genetica van de gastheer-parasiet interactie duidelijk worden gemaakt.

De resistentieveredeling is een belangrijke factor in het verschijnen van nieuwe fysiologische rassen en in de evolutie van de pathogeniteit.

In Amerika wordt de resistentieveredeling van tarwe als volgt uitgevoerd:

1. Nieuwe resistentiebronnen worden gezocht door grote collecties rassen en kruisingslijnen te toetsen.
2. Landbouwkundig waardevolle rassen worden gekruist met een reeks van resistentiegeniteurs; de kruisingsproducten worden enkele malen teruggekruist met de uitgangsrassen. Op deze wijze verkrijgt men voor ieder ras een reeks van landbouwkundig belangrijke lijnen die in vele eigenschappen sterk overeenkomen, maar die verschillen in de genetische samenstelling van hun resistentie.
3. Wanneer het programma tot zover is uitgevoerd, kunnen verschillende wegen worden gevolgd:
   a. Resistente vervangingslijnen kunnen worden gekweekt en in voorraad worden gehouden, teneinde een landbouwkundig waardevol ras, dat zijn resistentie verliest, te vervangen.
   b. Met behulp van een aantal in landbouwkundige eigenschappen goed overeenkomende lijnen, die in de genetische samenstelling van hun resistentie verschillen, kan men een samengesteld ras produceren. Hierdoor wordt het risico van grote opbrengstdervingen ten gevolge van epidemieën verkleind.

c. Men kan de verschillende vormen van resistentie distribueren over de verschillende landbouwgebieden, zodat ieder landbouwgebied zijn eigen type van resistentie bezit. Zo zal een eventuele epidemie tot slechts één landbouwgebied beperkt blijven.

De Amerikaanse werkwijzen kunnen niet zonder meer naar Europa worden overgebracht. Voor Europa lijkt de meest belovende toepassing van de nieuwe mogelijkheden het samengestelde ras.

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